ed epidermal layers (adaxial or ligular surface in dorsal leaves and abaxial or aligular surface in lateral leaves) consist of elongate tabular cells with numerous small plastids. Certain other features of the leaves of *S. martensii* do not exhibit a relationship to light. For example, stomates occur primarily on the aligular (abaxial) leaf surface regardless of orientation to light (Dengler, 1980).

Dengler (1983a, b) sought to determine the developmental basis for anisophylly in *S. martensii* by carefully following leaf initiation, development, and histogenesis. She concluded that, although the general pattern of growth is similar for both dorsal and lateral leaves, the two leaf types diverge early in development and can be distinguished at inception. She argued against Goebel's theory of developmental arrest to account for the differences between dorsal and ventral leaves. Goebel (1895) proposed that all leaves of a heteroblastic series share the same early stages of development and differ in mature form through a process of arrest at a particular developmental stage and subsequent divergence of ontogenetic pathways. In contrast, Dengler argued that the dorsal leaf of *S. martensii* should not be regarded as an arrested form of the ventral leaf, since critical morphological differences are initiated at inception. Two distinct leaf forms result, which can be distinguished in the primordial stage rather than differentiating late in development.

In a recent series of experiments with *S. kraussiana*, which exhibits anisophyllous dorsiventral shoots typical for section *Heterophyllum*, Bilderback (1984a, b) demonstrated the effect of the small dorsal leaves on the response of the shoot to phototropism and in maintaining a plagiotropic growth habit. He used excised shoot tips that were placed in sterile culture and oriented with respect to light. When placed in a normal position, with the dorsal leaves illuminated, shoot bending was slightly below the horizontal position, and the normal plagiotropic habit occurred (Bilderback, 1984a). Curvature resulted from asymmetric growth of the stem in a region just behind the apex, where cortical cells on the dorsal stem surface underwent greater elongation than ventral cortical cells. When the ventral surface was illuminated, the shoot exhibited a strong phototropic response so that the dorsal leaves eventually were reoriented toward light. The phototropic response was negated by application of phenylacetic acid (a known inhibitor of phototropism) to the dorsal leaves. Results of dark experiments indicated that the growth response was not affected by gravity.

Surgical removal of young dorsal leaves strongly inhibited phototropic curvature of the shoot (Bilderback, 1984b). Replacement of dorsal leaves with auxin in lanolin paste restored the phototropic response, whereas application of triiodobenzoic acid (TIBA), an auxin transport inhibitor, to dorsal leaves resulted in a significant reduction in phototropic stem curvature. The author concluded that phototropic sensitivity allows *Selaginella* to maintain its orientation with its environment. The dorsal leaves act as an auxin source to the dorsal portion of the stem, which results in greater cell elongation and stem bending. Light to the dorsal surface inhibits the bending, so that the shoot maintains its typical dorsiventral orientation.

LIGULE

Another interesting morphological feature in *Selaginella* is the ligule, a tiny appendage attached to the base of each leaf on the adaxial surface (Fig. 1). In addition to its universal occurrence in living species of *Selaginella*, the ligule has been described for extinct members of the genus, including *S. fraiponti*, a fossil of mid-Pennsylvanian age (Rock & Segal, 1973). The recent discovery (Grierson & Bonamo, 1979) of a ligule in *Leclercqia*, a fossil homosporous lycopsid from the Devonian, has resulted in a reevaluation of the concept that the ligule is always linked with heterosporous plants. Although the ligule in *Selaginella* has been the subject of numerous investigations, its function remains a mystery. It has been suggested that the ligule may function in secretion of mucilage or water, absorption of water, mucilage accumulation, production-collection-transport of materials, or that it may represent a vestigial organ (Horner et al., 1975).

Horner et al. (1975) examined the development of the ligule in *S. pilifera* and *S. uncinata* at the light microscope and ultrastructural levels. They divided the ligule into tip, neck, and basal regions (Fig. 1). They described the ligule of *S. pilifera* as being shaped like a curved hand; that is, the broad tip consisted of fingerlike unicellular papillae, the neck resembled appressed fingers 1–2 cells thick, and the base was broad and bulbous, like a swollen palm. In contrast, the ligule of *S. uncinata* was shaped like a slightly flattened bowling pin, with no distinct papillae. In agreement with earlier studies, Horner et al. (1975) pointed out the precocious development of the ligule and indicated that the entire structure stained intensely for RNA early in development, whereas only the polygonal basal cells of older ligules stained intensely. In the basal region, the bottommost layer of sheath cells

was separated from the leaf vascular strand by one or two layers of mesophyll cells. Thus, the vascular strand was not in direct contact with the ligule. The entire ligule was covered with a cuticle continuous with the cuticle on surrounding surfaces of the leaf.

In their ultrastructural study, Horner et al. (1975) noted that the cells of the ligule possessed plastids that contained only a few internal lamellae and that the ligule never became green. The authors agreed with Sigee (1974) that the central cells gave the appearance of highly active cells and that their ultrastructure was similar to that in certain plant secretory systems; that is, the cells were dense and contained numerous ribosomes, Golgi bodies and associated vesicles, mitochondria, and plastids. Although the presence of callose was noted in the polygonal base cells, the authors found no evidence for the secretion of mucilage.

The glossopodium and sheath cells (Fig. 1) differed anatomically from the central cells. At maturity the large glossopodial cells were vacuolate and were subtended by two layers of bricklike sheath cells. Prominent ingrowths occurred on the lower glossopodial wall and on the upper wall of the adjacent sheath cell. Horner et al. (1975) suggested that these cells with wall ingrowths might be involved in the movement of solutes. The walls common to the upper and lower sheath cells lacked ingrowths but contained numerous plasmodesmata. Although the ligule base was separated from the leaf vascular strand by one or two mesophyll cells, the authors pointed out that there is no reason to believe that the mesophyll cells would inhibit the movement of materials in either direction.

As had been found in previous studies, Horner et al. (1975) noted that ligule development and maturation occurred rapidly. In *S. uncinata* the tip and neck cells appeared to senesce soon after maturation, whereas the polygonal basal cells, glossopodium, and sheath cells remained unchanged for a number of dichotomies back from the tip.

Based on their observations on *S. uncinata* and *S. pilifera*, Horner et al. (1975) contended that the ligule is physiologically active and contains cells that may be involved in the movement of certain substances through the ligule. As another possibility, they suggested that the ligule may represent a vestigial organ that still retains certain properties of a once functionally active state.

In a series of studies, Sigee (1974, 1975, 1976) examined the structure and function of the ligule of *S. kraussiana*. In an ultrastructural study, Sigee (1974) noted that the central cells of the ligule displayed an extensive endoplasmic reticulum and Golgi system, which produced large numbers of Golgi vesicles. He proposed that the central cells could be involved in the elaboration or secretion of materials. A comparison with known secretory systems in other plants, however, suggested that the ligule is not active in the mass secretion of mucilage. He noted the presence of a continuous cuticle, which lacked cuticular pores and with no signs of rupture—further indications that the ligule is a nonsecreting structure.

Using histochemistry and light and transmission electron microscopy, Sigee (1975) was able to show that there was no significant accumulation of mucilage within the cells or on the surface of the ligule. He suggested that the Golgi system in the ligule, rather than secreting mucilage, contributed to cell wall formation. In another study, Sigee (1976) showed the incorporation of tritiated glucose into cells of the central region of the ligule, with particular accumulation in the Golgi bodies. The uptake and retention of label was cited as evidence that the Golgi bodies were active in the synthesis of complex carbohydrates, but did not pass these substances to the cell surface. Sigee (1976) concluded that the relatively inactive Golgi system in the ligule may be derived phylogenetically from a more active one and suggested that the ligule could be a vestigial organ, derived from a primitive secretory structure.

Jagels & Garner (1979) compared callose deposition in ligules of seven species of *Selaginella*. Using aniline blue stain and fluorescence microscopy, they determined that callose was localized in the basal region of the ligule and that the amount of deposition could be related to habitat. Species from dry, sunny habitats (the isophyllous *S. rupestris* and *S. densa* and the anisophyllous *S. lepidophylla*) exhibited heavy callose deposits, whereas species from moist, shady habitats (*S. kraussiana*, *S. martensii*, *S. apoda*, and *S. uncinata*—all anisophyllous species) had a light to moderate deposition of callose.

Recent evidence has been presented for the secretion of mucilage by ligules in several species of *Selaginella* (Bilderback, 1987). Putative mucilage bodies were shown to be associated with ligules of greenhouse-grown *S. kraussiana* and in ligules of *S. wallacei* and *S. oregana* from nature. When shoot tips of *S. kraussiana* and *S. douglasii* were grown in sterile culture with sucrose in the medium, massive amounts of mucilage were found around the apical meristem and coating the youngest leaves. The mucilaginous material in *S. kraussiana* was composed of protein and polysaccharide. In contrast, no mucilage was associated with ligules of *S.*

douglasii, *S. densa*, or *S. apoda* from nature, nor was mucilage produced when shoot tips of *S. wallacei*, *S. densa*, or *S. apoda* were grown in sterile culture. Because mucilage was found to be closely associated with the ligules of several species, Bilderback (1987) concluded that the ligule of *Selaginella* may be glandular.

In order to understand better the possible role of the ligule in mucilage secretion, Bilderback & Slone (1987) investigated the ultrastructure of the ligule in cultured shoot tips of *S. kraussiana*. Polysaccharide bodies similar to those seen in the mucilage believed to be secreted by ligules also were observed in apical cells of ligules from cultured shoot tips. Although no pores or breaks in the cuticle were seen, the cuticle of the apical cells was distended and separated from the cell wall, and electron-dense granules were present in the space thus formed. Although the apical cells lacked dictyosomes, they did possess dilated endoplasmic reticulum. Dictyosomes were present in the cells of the basal portion of the ligule. The ultrastructure of the ligule was compared to that of secretory structures in angiosperms, and Bilderback & Slone (1987) concluded that the ligule in *S. kraussiana* is a structure that produces and secretes extracellular mucilage.

Kohlenbach & Geier (1970) used selective staining of leaves with berberine sulfate to study the function of the ligule in *S. kraussiana* and presented evidence that the ligule is a site for absorption of liquids. They suggested that the ability of the ligule to absorb liquids is related to special qualities of the thin cuticle at the ligule apex.

Lafont & Lemoigne (1965), using light microscopy, reported a system of canals in the rather large ligule of *S. willdenovii*. They described a principal canal and occasional connecting secondary canals. The canals were reported sometimes to open directly to the surface of the ligule. The canals occurred only in the basal part of ligules in an advanced stage of development. Although the exact significance of this system of canals is unknown, the authors suggested that they might serve as a pathway for the emission of products to the exterior environment, and that a role in water absorption for the ligule is debatable. The ultrastructure of the plastids in the ligule of *S. willdenovii* was also studied by Lafont & Lemoigne (1966). The small achlorophyllous plastids were found to contain vacuoles and associated amorphous material, and the authors suggested that these plastids might be associated with a secretory function.

Despite the considerable attention that has been paid to the ligule of *Selaginella*, the function remains a mystery. Suggestions that it is an organ involved in water absorption, water or mucilage secretion, mucilage accumulation, or the production-collection-transport of materials have been made, as well as the possibility that the ligule is a vestigial organ (Horner et al., 1975). Much of the evidence presented to date is contradictory, so that a definitive interpretation for the function of the ligule must await further investigation.

FOLIAR EPIDERMAL ORNAMENTATIONS

Recent studies have shown the presence of distinctive epidermal ornamentations in leaves of *Selaginella* species. These ornamentations are evident as so-called warty cells and teeth that are prominent along the leaf margins (Fig. 1). Waterkeyn & Bienfait (1967) first described the interesting method of development of these cells in leaves of *S. kraussiana*. Using the dyes resorcinol blue and aniline blue and fluorescence microscopy, they were able to show that the outer walls of these specialized cells undergo callose deposition, which is then gradually degraded and replaced with silica. Differentiation in leaves of *Selaginella* is basipetal, so that the development of marginal teeth and warty cells can be followed sequentially. Thus, in a differentiating leaf, the teeth and warty cells at the leaf apex possess silica walls; in subjacent regions of the leaf, teeth and warty cells contain both callose and silica; and at the base of the leaf, these cells possess callose but no silica in their outer walls. Concerning a possible function for these distinctive cells, Waterkeyn & Bienfait (1967) noted that plants that are strongly mineralized often have a particularly high rate of cuticular transpiration, and they suggested that the marginal warty cells and teeth might somehow be involved in the control of foliar transpiration in *Selaginella*.

Waterkeyn et al. (1982) expanded their study of foliar emergences in *S. kraussiana* to similar structures in several angiosperms, including *Cannabis sativa*, *Urtica dioica*, *Campanula persicifolia*, and *Blumenbachia hieronymi*. In all of these cases it was shown that a callose phase occurred before or during silicification of the walls of these epidermal cells. They determined that callose deposition resulted in a thinning of the wall and overlying cuticle, and that the fluorescent dye, berberine sulphate, accumulated in the cells possessing callose, but not in those that had become silicified. They also presented evidence that these epidermal cells are regions where absorption is favored owing to the greater permeability of the

cuticle. Their results indicated that the epidermal appendages in the plants investigated, including the foliar marginal warty cells and teeth of *S. kraussiana*, are regions of active transpiration. Based on their study, they suggested that callose might play two roles: (1) to control somehow the movement of water by a nonosmotic mechanism; and (2) to provide a favorable matrix for silica deposition during wall formation.

LeCoq et al. (1973) used scanning electron microscopy, fluorescence microscopy, and the electron microprobe to trace the development of the marginal teeth and warty cells in *S. kraussiana* and confirmed the earlier observations of Waterkeyn & Bienfait (1967) of a callose phase that preceded silicification in these cells. They also noted that, in addition to marginal teeth and warty cells, certain other cells of the leaf epidermis possessed mamillae, smaller silicified leaf ornamentations. They also found that the outer cell walls of the entire leaf epidermis eventually became covered with a continuous layer of silica. Robert et al. (1973) continued the study of leaf ornamentations in *S. kraussiana* by using transmission electron microscopy. As a result of their investigation, they proposed five phases of silicification in the external walls of leaf epidermal cells in *S. kraussiana*: (1) a pectic-cellulose phase; (2) a callose phase during which the marginal teeth and warty cells achieve their final shape and size; (3) a cellulosic phase, which isolates a callose plug; (4) silicification of the teeth and warts, during which callose is gradually replaced; and (5) a new phase of silicification over the entire outer wall.

Robert & Laroche (1979) later described the development of the marginal warty cells of *S. kraussiana* in detail. As seen with the transmission electron microscope, a wart first appeared as a raised area resulting in a space between the outer cell wall and the plasmalemma. This space, the central region of the wart, then became filled with callose. Below this space, the cytoplasm was rich in endoplasmic reticulum, which the authors suggested may be important in the formation of callose. Once the wart attained its final size, a new pectocellulose wall was formed beneath the raised area, thus isolating the callose plug from the cytoplasm. During these changes in wall structure, the cuticle covering the wart became thinner and was structurally disrupted. These localized disruptions of the cuticle appeared to the authors to result in an increased flow of water at these particular points (Robert & Laroche, 1979). Finally, there was a breakdown of the central callose plug, accompanied by a gradual replacement of the callose with silica.

Dengler & Lin (1980), using scanning electron microscopy and X-ray microanalysis, studied the distribution of silica in the ventral (lateral) leaves of *S. emmeliana*. High levels of silica were found in the marginal warty cells (termed "marginal sclereids" by the authors) and in approximately half of the abaxial epidermal cells. Stomates were confined to a broad band of cells on the abaxial (aligular) surface overlying the single vascular strand. Although most cells of the stomatal band did not accumulate significant amounts of silica, approximately 6% of the stomata possessed high levels of silica and exhibited a constricted aperture. Epidermal cells that were unprotected by adjacent ventral leaves and were thus exposed to light were the ones that developed warty projections and accumulated silica. Dengler & Lin (1980) suggested that higher rates of transpiration might be expected from the exposed portion of the leaf, which could account for the observed pattern of silica distribution. The authors concluded that although the function of silica in *Selaginella* is unknown, it is possible that it may play an important role in support of the leaf. They also pointed out that others (Kaufman et al., 1972) have suggested that hydrated silica gel in the epidermal walls may provide water to a leaf or stem during periods of drought or when transpiration causes loss of turgor.

Based on a comparison of several species of *Selaginella*, Bienfait & Waterkeyn (1974) concluded that the morphology and distribution of marginal teeth and warty cells in leaves could be useful in taxonomic determinations.

Although the structure of these distinctive leaf epidermal cells of *Selaginella* has been carefully documented, their function has yet to be determined. Based on the recent studies cited above, a role in water economy would seem to be a reasonable possibility.

MONOPLASTIDY

Another interesting feature of leaf anatomy in *Selaginella* pertains to the chloroplasts of the epidermal cells. Typically for leaves of *Selaginella*, the epidermal cell layer directed toward light (aligular surface in dorsal leaves, ligular surface in lateral leaves) is composed of conical or bowl-shaped cells, each containing a single large chloroplast (Fig. 1). In recent years there have been several studies on the structure and development of these plastids (Jagels, 1970a, b; Webster & Tanno, 1980; Tanno & Webster, 1982b). Despite their size, these chloroplasts exhibit normal ultrastructure, with distinct grana, stroma, and starch grains. It would appear

that these plastids represent the major light-absorbing region of the leaf, and also show a remarkable adaptation for shady habitats. It has been shown that these plastids are able to move in response to light direction and intensity (Zurzycki & Zurzycka, 1951; Mayer, 1971; Haupt, 1973, 1982). For example, when leaves of *S. martensii* are exposed to diffuse daylight, the chloroplast lies at the base of the cell and occupies the whole area of the cell. If the leaf is illuminated with intense white light, the first chloroplast movements are detectable after 10–20 minutes. The chloroplast moves to a side wall, leaving the base and opposite wall uncovered. This movement of the chloroplast onto the side walls is accomplished after two or three hours (Zurzycki & Zurzycka, 1951). According to Haupt (1973), who discussed chloroplast movement in several plants:

> The biological significance of these light-dependent arrangements seems self-evident: The low intensity arrangement enables the chloroplasts to absorb as much light for photosynthesis as possible, but the high intensity arrangement protects them against the absorption of damaging amounts of light.

In recent years there has been considerable interest in monoplastidy and its association with cell division mechanisms. As part of a series of studies on cell division mechanisms in monoplastidic plants, Brown & Lemmon (1984, 1985, 1990) have pointed out that among vascular plants, *Selaginella* and *Isoetes* possess meristematic cells that are monoplastidic. Cell division in such cells is subject to certain constraints that result in each daughter cell receiving a plastid, thereby avoiding the apoplastidic condition. In a recent study of cell division in root meristems of *Selaginella* and *Isoetes*, Brown & Lemmon (1984) noted the precise orientation of the dividing plastid relative to the preprophase band. Specifically, the plastid is oriented with the long axis perpendicular to the preprophase band, and the isthmus of the dividing plastid is in the plane of the preprophase band and, in turn, the mitotic equator. The regular positioning of the plastid during cell division is obviously an important part of morphogenesis in monoplastidic cells. The orientation of both the preprophase band and the dividing plastid predict the plane of cell division.

In another study, Brown & Lemmon (1985) examined cell division and plastid movements in stomates of *S. erythropus*. They noted the same spatial relationship between the preprophase band and dividing plastid in the guard mother cell as was found for root meristematic cells (Brown & Lemmon, 1984), but they also described postcytokinetic plastid migrations during guard cell differentiation. The authors (Brown & Lemmon, 1985) stated that plastid behavior in developing stomates of *Selaginella* is the most complex yet demonstrated for monoplastidic cells. The observed plastid movement in guard cells is related to cytoplasmic polarity and is clearly a different phenomenon than photo-induced plastid movement seen in normal photosynthetic leaf cells of *Selaginella*. These observations suggest the need for further study to determine the mechanisms of plastid movements in *Selaginella*. The recent studies of variation in cell division mechanisms in monoplastidic plants, which include numerous algae, certain bryophytes, and, among vascular plants, *Isoetes* and *Selaginella*, seem certain to have important evolutionary implications.

ROOT (RHIZOPHORE)

One of the most controversial organs of *Selaginella* is the leafless cylindrical structure arising at the angle of shoot branching (Fig. 1). This structure is positively geotropic, green for much of its length, and lacks a root cap and root hairs until it strikes the soil. In addition, the angle-meristem from which it arises may, under certain conditions, develop into a leafy shoot. Nageli & Leitgeb (1868) coined the term "rhizophore" (root bearer) for this organ, since they believed true roots were produced endogenously behind the tip of the rhizophore. Since then, the morphological nature of this curious organ has been a source of continued debate. Over the years, the rhizophore has been interpreted as a modified root, shoot, or an organ sui generis.

In a series of studies involving four species, Webster & Steeves (1963, 1964, 1967) examined the morphology and development of the organ in question, and determined that it is a root throughout its development. They provided evidence that refuted the early interpretation that endogenous roots are produced behind the tip of a so-called rhizophore. In *S. kraussiana* (anisophyllous), *S. densa* and *S. wallacei* (both isophyllous), all species with a creeping habit, root caps are formed when the root is less than 1 mm long. In *S. martensii*, an ascending species, the leafless structure arising at the angles of shoot branching grows for several centimeters before forming a root cap. Root caps are produced as the tips of the branching root strike the soil. In all four species root hairs are produced as the tips enter the soil, soon after root cap formation. The root cap is formed when the apical cell of the root meristem, in addition to producing

lateral segments, begins to cut off cells from its distal face as well. Thus no evidence for a "root bearer" (rhizophore) was found by Webster and Steeves, and the organ was interpreted as a root.

In a recent study of *S. uncinata*, Imaichi & Kato (1989) refuted the interpretation by Webster & Steeves (1963, 1964, 1967). According to Imaichi & Kato (1989), subterranean roots of *S. uncinata* are derived endogenously behind the apex of a rhizophore. The initial of the rhizophore apex is divided by periclinal divisions into rectangular and prism-shaped cells and becomes indistinguishable from neighboring cells. Apical cells of endogenous roots are then formed from inner cells near the apex of the rhizophore. A similar interpretation for endogenous root origin behind the rhizophore apex resulted from the study of three large tropical species with branched rhizophores (Imaichi & Kato, 1991). Their studies thus support the earlier view of Bruchmann (1905).

Despite considerable study of the leafless cylindrical structures that arise at the angles of shoot branching in *Selaginella*, the morphological interpretation of these structures remains an open question. Final resolution of the root–rhizophore controversy must await further investigation.

Webster & Jagels (1977) investigated the development of aerial roots in *S. martensii* grown under experimental conditions. Aerial roots (capless, hairless, and with green tips) were directed into moist bottles so that the tips were prevented from touching a solid surface as they grew through the air. Under the humid conditions produced inside the bottle, the roots grew, branched dichotomously, and formed root caps followed by root hairs. During development there was a gradual loss of pigmentation in the root apices, so that by the time caps and hairs were formed, the tips were colorless. Sections showed that the green color of aerial root tips resulted from chloroplasts in the cortex, whereas the same region in colorless root tips (with caps and hairs) contained amyloplasts. Developmental changes in plastid structure were also followed with the transmission electron microscope. From their observations, Webster & Jagels (1977) concluded that the leafless cylindrical organs arising from angle-meristems of *S. martensii* are roots, and they refuted the concept of a rhizophore. They also suggested that the presence of a root cap may be necessary in order for root hairs to be formed and showed that neither physical contact nor darkness are necessary conditions for caps and hairs to be formed.

A study by Grenville & Peterson (1981) provided further details of the root cap and apical meristem in aerial and subterranean roots of *S. kraussiana*. They noted the presence of a thick cuticle over the surface of the bulbous root cap of the aerial root and suggested that its role might be to prevent desiccation as the root grows through the air toward the soil. They also noted a lack of statolith starch in the root cap of aerial and subterranean roots, both of which are positively geotropic. They pointed out that a study of the mechanism of geotropism in *Selaginella* is needed. Although their study showed certain structural differences between aerial and subterranean roots of *S. kraussiana*, Grenville & Peterson (1981) concluded that the organ is a root throughout its development, an interpretation that agrees with that of Webster & Steeves (1964).

Bilderback (1985, 1986) recently reported on tropic responses of rhizophores (aerial roots) of *Selaginella kraussiana*. When branching shoot tips bearing young rhizophores were oriented in a horizontal but inverted position on nutrient agar and illuminated from above, erect rhizophores grew away from light and toward gravity. In darkness, rhizophores grew in wide arcs toward gravity. Bilderback (1985) concluded that the weak geotropic response of the rhizophore is intensified by light. In another study, Bilderback (1986) oriented shoots so that the rhizophores were in a horizontal position, and illumination was from below. After five hours the tips bent 90° away from light. When placed in darkness, the rhizophore tips bent only 30° toward gravity. Removal of 2–3 mm of the tip prevented bending of the rhizophore away from light; however, decapitated rhizophores treated with abscisic acid in lanolin did bend away from light. Bilderback (1986) suggested that the strong negative phototropic reaction of the rhizophore may be mediated by abscisic acid.

Karrfalt (1981) studied the root system of *S. selaginoides*. As in other species of *Selaginella*, the first three roots are produced from the young sporeling. However, unlike typical species of *Selaginella*, subsequent roots arise from a swollen root-producing meristem at the base of the hypocotyl, and no roots are formed from angle-meristems along the shoot. Thus, a total of only 8–10 roots are produced in *S. selaginoides*. Karrfalt (1981) considered earlier comparisons of *S. selaginoides* with certain fossil arborescent lycopsids (e.g., *Stigmaria*) as invalid; rather, he considered *S. selaginoides* to represent a condition in which the juvenile (sporeling) method of root formation, which normally accounts for only the first three roots, is retained in the adult plant. A thorough reinvestigation of the morphology of *S. selaginoides*, in-

cluding both vegetative and reproductive organs, is in order. Whether the unusual morphology seen in this isophyllous species represents a primitive or an advanced condition is not clear at this time. The relationship of *S. selaginoides* to the other isophyllous species of *Selaginella* and to the genus as a whole is poorly understood and in need of further investigation.

The angle-meristem of *Selaginella* is one of the few examples of a truly undetermined meristem—one that has the potential to develop as either a root or as a shoot (Halperin, 1978). This morphogenetic plasticity may be indicative of a primitive nature and thus have a bearing on certain phylogenetic questions in *Selaginella*. Several recent studies have examined the developmental potential of angle-meristems.

Webster (1969) examined the effect that auxin has on angle-meristem development in *S. martensii*. In this study, Y-shaped shoot segments, each bearing a dorsal and a ventral angle-meristem, had either plain lanolin or lanolin containing auxin applied at the distal cut surfaces. In the presence of exogenously supplied auxin, angle-meristems developed as roots, whereas in the absence of auxin, shoots were formed. The results also showed that precocious development of a ventral angle-shoot could influence the dorsal angle-meristem to develop as a root. Destroying the ventral angle-meristem by puncturing resulted in development of a dorsal angle-shoot. Presumably the ventral angle-shoot acted an an auxin source to control dorsal development.

Cusick (1953) analyzed the shoot system of *S. willdenovii* and noted that at each bifurcation of the main shoot axis a dorsal and a ventral angle-meristem are present. For any given shoot branching, the ventral angle-meristem is the first to develop and produces a rhizophore (aerial root); the corresponding dorsal angle-meristem is delayed in its development and produces a shoot. In isolated shoot segments of *S. willdenovii*, Cusick (1954) was unable to alter, by surgical treatments, the position of leaf primordia arising on ventral angle-shoots. He reasoned that growth centers for leaf primordia were already present in the dormant angle-meristem; therefore auxin, either from the intact axial shoot or applied distally to isolated stem segments, must allow the development of the apical but not appendicular growth centers, and a rhizophore results. In the absence of auxin, appendicular growth centers are no longer inhibited, leaf primordia develop, and an angle-shoot results. Based on his experiments with *S. willdenovii*, Cusick (1954) suggested that, in ontogeny, the angle-meristem is basically an embryonic shoot, and rhizophore formation involves a secondary change in the pattern of growth.

In a series of articles, Wochok & Sussex (1973, 1974, 1975, 1976) further examined morphogenesis in the root and shoot system of *S. willdenovii*. Using ^{14}C-indoleacetic acid they traced auxin transport in the shoot system and developed a hypothesis for auxin regulation of angle-meristem development in *S. willdenovii*. As will be recalled from the previous work by Cusick (1953, 1954), at each bifurcation of the main shoot axis, a dorsal and a ventral angle-meristem are formed. The ventral angle-meristem is the first to develop and forms a root; the dorsal angle-meristem develops later and produces a shoot. In a study of auxin transport in the stem, Wochok & Sussex (1973) found that auxin transport was polar through the stem axis, but in the region of shoot branching there was lower auxin concentration on the ventral side of the shoot and a higher concentration on the dorsal side. These findings were related to the observed development of angle-meristems. Wochok & Sussex (1973) hypothesized that in the region just behind the shoot apex, the high auxin concentration inhibits development of both angle-meristems. Further behind the apex, the reduced auxin concentration on the ventral side initiates development of the ventral angle-meristem, and the auxin level results in determination as a root. In branchings still further behind the apex, the auxin concentration to the dorsal surface is decreased, and the dorsal angle-meristem is stimulated to develop as a shoot because of a lower auxin level. This hypothesis was further related to the complex stelar pattern in *S. willdenovii*, which includes a tristelic condition in the main axis of the shoot.

An examination of auxin transport in the root showed that auxin moved predominately in an acropetal direction (Wochok & Sussex, 1974). This was cited as physiological evidence that the leafless cylindrical organ arising at the angles of shoot branching in *S. willdenovii* is a root and not a shoot.

In another study of angle-meristem development in *S. willdenovii*, Wochok & Sussex (1975) used triiodobenzoic acid (TIBA), an auxin inhibitor. When TIBA was applied in lanolin paste around the stem in a region just behind the shoot tip of intact plants, both dorsal and ventral angle-meristems in the vicinity developed as leafy shoots. When dorsal angle-meristems were excised and grown in sterile culture, they developed as leafy shoots on an auxin-free medium and as roots on a medium containing auxin. Dorsal angle-meristems transferred after ex-

cision from auxin-free to plus-auxin medium on successive days showed an increasing tendency to develop as shoots. From these results the authors suggested that dorsal angle-meristems undergo a change in developmental potential. That is, after 1–3 days in culture most dorsal angle-meristems could still be influenced by exogenous auxin to develop as roots. However, after 5 days a majority of dorsal angle-meristems had been determined as shoots and could not be "redetermined" by auxin as roots.

Wochok & Sussex (1976) also studied the developmental potential of excised root tips of *S. willdenovii*. When roots approximately 20 mm or less in length were grown in sterile culture on an auxin-free medium, approximately 20% of them developed as leafy shoots. When root tips were grown on a medium containing auxin, only roots were produced. Thus it was shown that auxin prevents redetermination of the root apex as a shoot, and the reason redetermination does not occur in the intact plant may be that auxin is transported toward the root tip where it exerts its control.

Finally, Jernstedt & Mansfield (1985) used a chemical approach to interpret the nature of the so-called rhizophore. Using two-dimensional gel electrophoresis, they compared polypeptides from the vegetative organs of *S. kraussiana*. Of the more than 600 polypeptides resolved, 18% were found in all four vegetative organs (leaves, stems, roots, and rhizophores). Comparisons between pairs of organs revealed that stems and rhizophores showed the greatest similarity with 58% of their polypeptides in common, while for rhizophores and roots, 42% of their polypeptides were similar. They also found that stems and rhizophores had the largest number of polypeptides unique to a pair of organs (95), while rhizophores and roots shared fewer unique polypeptides (5). Jernstedt & Mansfield (1985) concluded that, at the abundant gene-product level, stems and rhizophores are more similar than are rhizophores and roots. Further, the results contradict the view that the rhizophore is simply an aerial phase of the root system, but, rather, indicate that the rhizophore is sufficiently distinct to be placed in the organ category. Finally, the results refute the interpretation that rhizophores and roots are homologous organs.

The above studies indicate that organography in *Selaginella* is somewhat plastic, so that the same meristem (angle-meristem) may develop as either a root or a shoot, depending on the conditions of growth. This, along with the other unusual features of the aerial root or rhizophore indicate that in *Selaginella* root and shoot are not so distinct and suggest a somewhat primitive state of organography. Such a conclusion seems reasonable in view of the antiquity of the genus. In this connection, it should be pointed out that in certain Devonian fossils, branchlike structures (called axillary tubercles) have been found associated with angles of shoot branching. Banks & Davis (1969) hypothesized that the axillary tubercles of *Gosslingia* and *Crenaticaulis* may represent rhizophorelike branches similar to those in modern *Selaginella*. However, in a general discussion of axillary tubercles, Edwards (1970) suggested that the structure probably represents the base of a branch, which was either abscised prior to preservation or was lost during preservation.

Reproductive Morphology

HETEROSPORY

An important feature in the reproductive biology of *Selaginella* is heterospory (Fig. 1). Despite the fundamental importance of heterospory to plant evolution, neither the physiological basis nor the origin of this phenomenon are presently well understood. Sussex (1966) has discussed the origin and development of heterospory in general, and Pettitt (1971, 1977) has investigated certain aspects of heterospory for *Selaginella*, specifically, megasporocyte degeneration and post-meiotic regression of megaspores and microspores. Recently, Haig & Westoby (1988) proposed a theoretical model to account for the origin of heterospory. However, despite these and other discussions, many critical questions about heterospory remain unresolved.

SPORANGIAL DEVELOPMENT

Horner & Beltz (1970) studied the early stages of sporogenesis in *S. pilifera* and compared developing microsporangia and megasporangia with respect to certain features. They noted that, in pairs of sporangia, megasporangia were slightly larger than microsporangia from an early stage of development. In the microsporangium, sporogenous tissue stained intensely for RNA, whereas in the megasporangium of corresponding age, only a single cell of the sporogenous tissue stained. Furthermore, whereas each sporogenous cell in the microsporangium was surrounded by callose, in the megasporangium only the RNA-positive (functional) sporocyte developed a callose wall. Based on these findings, the authors suggested that the formation of a callose wall around the single functional sporocyte serves to isolate that cell in the sporan-

gium, resulting in differentiation in a new direction. A causal mechanism for the determination of megasporogenesis versus microsporogenesis is as yet unclear, however.

Using length of sectioned sporangia as an index, French (1972) examined growth relationships in developing megasporangia and microsporangia of *S. bigelovii*. Strobili of *S. bigelovii* usually contain two vertical rows of megasporangia and two rows of microsporangia, and, at each node, a megasporangium is opposite a microsporangium. French (1972) discovered that for a pair of decussate sporangia, prior to sporocyte formation the megasporangium was larger and elongated more rapidly than the corresponding microsporangium. Also, although there was an increase in the number of sporogenous cells in both sporangial types in early development, this increase in sporogenous cell number ended at a lower growth index in megasporangia than in microsporangia. Thus the differences in growth relationships observed by French (1972) indicate that events that ultimately lead to the development of microsporangia and megasporangia occur prior to the onset of sporocyte degeneration.

Brooks (1973) studied the effects of ethylene on the determination of sporangia in *S. wallacei* and *S. pallescens*. In plants sprayed with distilled water, strobili produced a high proportion of microsporangia, whereas plants sprayed with Ethephon, an ethylene-releasing compound, produced a high proportion of megasporangia. Brooks (1973) speculated that sporangial determination in *Selaginella* may rely on the effects of ethylene on plant cells. He noted that ethylene is known to inhibit or retard cell division as well as accelerate or induce cell degeneration in certain plant tissues. Therefore, a high endogenous level of ethylene could result in one less division in cells of the sporogenous tissue, producing fewer sporocytes per sporangium, and in the degeneration of most of them. Eventually sporocyte degeneration would result in one functional megasporocyte, which would produce four megaspores by meiosis. In the absence of an inhibitory level of ethylene, the final cell division would occur in the sporangium, followed by very little sporocyte degeneration, and ultimately result in numerous sporocytes in a microsporangium. Further work is necessary to prove this hypothesis, and future investigations should include the effects of other growth regulators on sporangial development.

Horner & Arnott (1963) examined sporangial arrangement in strobili from 30 North American species of *Selaginella* and described four patterns:

I. Basal megasporangia and apical microsporangia;
II. Two vertical rows of microsporangia and two vertical rows of megasporangia;
IIa. Two vertical rows of microsporangia and two vertical rows containing a mixture of microsporangia and megasporangia;
III. Wholly megasporangiate strobili.

They concluded that arrangement of sporangia can serve as a taxonomic tool. Of particular interest is *S. rupestris*, which exhibits patterns I and III; the populations exhibiting these two patterns can be separated geographically. Pattern I plants occur in the Appalachian mountain region and are presumably sexual, whereas Pattern III plants occur throughout the rest of the range and are apomictic. Horner & Arnott (1963) also suggested that the primitive condition is represented by Pattern I, from which the other patterns are derived.

An unusual variation of sporangial development was reported by Webster (1974). In *S. umbrosa* grown under greenhouse conditions, cones were microsporangiate but also exhibited an abundance of abortive sporangia. In addition, occasional small green vegetative outgrowths ("sporangioids") were found in the position of sporangia. These small cylindrical structures contained tissues resembling epidermis and cortex, as well as a central strand of tracheids. The exact nature and significance of sporangioids remain to be determined, as are the possible factors that account for their occurrence.

Recent studies on the morphology of microsporangia in *Selaginella* have provided insight into mechanisms of spore dispersal. Somers (1982) examined the microsporangium of series *Articulatae*, a group of approximately 40 species including *S. kraussiana* and *S. diffusa*, and concluded that the microsporangium in *Articulatae* is more complex than that found in the nonarticulate species. The microsporangium of *Articulatae* is characterized by two broad annuloid bands of thick-walled cells that play an important role in dehiscence. The presence of these bands suggests a more advanced condition not found in the microsporangium of other species of *Selaginella*. Somers (1982) argued that the highly developed microsporangium, together with several other characteristics, is sufficient to elevate the *Articulatae* to the status of subgenus.

In an examination of 53 species of *Selaginella*, Koller & Scheckler (1986) recognized five types of microsporangia that exhibit three spore dispersal mechanisms. In the passive type, there is little cell modification among the cells of the sporangium.

Dehiscence occurs along the distal surface and continues down the sides, resulting in two valves that bend outward, and the microspores simply sift out passively between the two valves. Most species exhibiting this mechanism are isophyllous and inhabit xeric environments. *Selaginella wallacei* is an example of the passive type of microsporangium. The spore-ejector type relies on a distinct area of dead water-filled cells within the sporangial wall. Koller & Scheckler (1986) recognized two subtypes within this category: the central subtype, characterized by an ovoid region of dead water-filled cells in the center of each valve; and the basal subtype, characterized by a reniform region of dead water-filled cells in the basal half of each valve. In each subtype, sporangial cells exhibit uneven wall thickenings resulting in active dispersal of microspores. As the sporangium dries and dehisces, the two valves bend away from each other, sometimes reaching an angle between them of 150°. The valves then snap back toward their original positions, ejecting a large portion of microspores. The valves may reflex and snap several times, effectively ejecting all the spores from the sporangium. After dehiscence is complete, the cells previously filled with water contain gas bubbles. The spore-ejector type of sporangium was observed in a number of anisophyllous tropical or subtropical species. *Selaginella emmeliana* is an example of the central subtype, and *S. plana* represents the basal subtype.

The sporangium-ejector type was found only in series *Articulatae* and was described previously by Somers (1982). The prominent feature of this sporangial type is the raised band of large cells extending around the sporangium. Koller & Scheckler (1986) noted that these cells are dead and water-filled, with uneven thickenings. At the time of dehiscence the two valves bend with such force that the microsporangium is torn from the strobilus and ejected for a distance up to 20 cm. A series of snapping motions completes spore ejection from the dispersed microsporangium. Once dehiscence is complete, the raised band of cells contains gas bubbles instead of water. Koller & Scheckler (1986) distinguished two subtypes based on minor anatomical differences, with *S. kraussiana* considered to be distinct from other members of *Articulatae*.

The authors suggested that the spore-ejector types have a dispersal mechanism similar to that of a fern leptosporangium, which relies on an annulus of distinctive cells. It was further suggested that the dispersal mechanisms described, particularly the sporangium-ejector type, enhance outcrossing in *Selaginella*. The passive type, which results in spores shed near the base of the parent plant, would be more likely to restrict the amount of outcrossing.

A recent study by Page (1989) described the dispersal mechanisms for both the microsporangium and megasporangium of *S. selaginoides*. Whereas microspore dispersal is passive in this species, megaspore dispersal is active, and, under experimental conditions, may result in discharge of megaspores for distances of over 2 m from the parent cone.

The studies by Somers (1982) and Koller & Scheckler (1986) have added significantly to our understanding of microspore dispersal in *Selaginella*. Further studies comparing dispersal mechanisms for both microsporangia and megasporangia of the same species, such as the recent investigation by Page (1989), are needed.

GAMETOPHYTE DEVELOPMENT

The gametophyte generation of *Selaginella* has received far less attention than the sporophyte. The small size of the endosporic microgametophytes and megagametophytes makes them more difficult to study and perhaps gives the impression that there is little variation in gametophyte morphology throughout the genus. In recent years, Robert has studied the development of the gametophytes of *S. kraussiana* in some detail. In his study of the microgametophyte of *S. kraussiana*, Robert (1973) described a two-staged ontogeny: (1) the formation of the antheridium and divisions resulting in a number of spermatogenous cells (spermatids), and (2) the differentiation of spermatids into spermatozoids. The mature microgametophyte consists of a single lenticular prothallial cell and an 8-celled antheridial jacket surrounding 256 spermatids. This study of the general organization of the male gametophyte was followed by a detailed description of spermatogenesis (Robert, 1974). The mature spermatozoid is 25 μm in length with two asymmetrical flagella. The organelles in the narrow sperm are linear. These include an anterior centriole, an elongate mitochondrion, and a nucleus. Toward the posterior pole is a posterior centriole and flagellum, a plastid, and a mitochondrion. In comparing the sperm of *S. kraussiana* to sperm in other archegoniates, Robert (1974) noted similarities to those of bryophytes. On the other hand, the sperm of *S. kraussiana* does not seem to have features in common with other pteridophytes, a conclusion also reached in an earlier study by Yuasa (1933).

Robert (1971a, b, 1972a) also provided a de-

tailed account of megagametophyte development in *S. kraussiana*. The megagametophyte of this species is unusual in that a thickened diaphragm divides the gametophyte into two distinct regions: the reproductive tissue from which archegonia and rhizoids form, and a food reserve region rich in lipids and proteins (Robert, 1971a). Robert went on to describe these regions in detail (Robert, 1971b, 1972a). He pointed out that, although large numbers of archegonia are formed, at any given time only one or two, sometimes none, have their necks open and thus are capable of being fertilized. He also described certain complexities exhibited by the egg, features not found in the eggs of other archegoniates. During oogenesis there is a redistribution of organelles, resulting in a marked polarity of the mature egg. There is an apical region of mitochondria, a peripheral and median region of Golgi bodies, and a basal region rich in endoplasmic reticulum. The plastids that occur around the nucleus also undergo certain changes during oogenesis. He also noted the occurrence of certain structures of undetermined origin. The result is a highly polarized egg cell of considerable complexity, the significance of which will be discussed later.

Wetmore & Morel (1951) were able to maintain sterile cultures of megagametophytes of *S. pallescens* and *S. flabellata*. They cultured the megagametophytes on Knudson's medium supplemented with 2% glucose and a mixture of vitamins. At the end of six months a globular mass of tissue approximately 1 cm diam. was obtained. By subculturing every three months they were able to maintain the tissue cultures for two years. Under the culture conditions employed, the prothallus lost its normal organization; that is, after their initial appearance, rhizoids and archegonia failed to be produced, and only unpigmented parenchyma cells were formed. The culture was thus similar to higher plant tissue cultures lacking organization, i.e., a callus.

Bruchmann (1912) studied embryology in a number of species of *Selaginella*, including *S. kraussiana*. The embryology of *S. kraussiana* is of particular interest because of certain unusual developmental features. Soon after fertilization of the egg, the basal wall of the archegonium elongates to form a tube. This "embryo tube" carries the zygote to the center of the reserve tissue where the embryo is initiated. Robert (1972b) speculated that this unusual development may result from certain structural complexities of the egg of *S. kraussiana* discussed above (Robert, 1972a). Further embryological studies of *Selaginella* using modern techniques are needed because, as noted by Gifford & Foster (1989), most of our present knowlege is based on a few early studies.

Finally, recent studies (Webster, 1979; Webster & Tanno, 1980; Tanno & Webster, 1982a, b) have used artificial crossing techniques to determine the inheritance of pigmentation in *Selaginella*. In *S. kraussiana* var. *aurea*, the *aurea* character is controlled by a single nuclear gene exhibiting incomplete dominance, whereas *S. martensii* forma *albovariegata*, a variegated variety, exhibits maternal cytoplasmic inheritance of pigmentation. The crossing technique (Webster, 1979) used in these studies allows for direct observation of certain aspects of the life cycle of *Selaginella* and raises several questions for future investigations. For example, the most dramatic feature observed during hybridization experiments with *Selaginella* is the strong chemotactic response. Almost immediately after megagametophytes and sperm are mixed in a droplet of water on a depression slide, attraction of sperm to the archegonial region of the megagametophyte can be detected with the light microscope. Within minutes, a sizable cloud of swimming sperm is visible around the archegonia. The chemical nature of the chemotactic principle in *Selaginella* has yet to be identified. Preliminary observations (Webster, unpublished) suggest that the chemotactic response is rather general, because for example, sperm of *S. kraussiana* are readily attracted to megagametophytes of *S. martensii*, an unrelated species (and sporelings fail to result). More detailed studies of the specificity of the chemotactic response in *Selaginella* should yield interesting results. Also, the details of fertilization have yet to be examined; this would be an ideal subject for an ultrastructural study.

Concluding Remarks

The genus *Selaginella* has existed since the Lower Carboniferous (Bierhorst, 1971). Today, this remarkable assemblage of approximately 700 species is distributed worldwide and occupies a wide range of habitats from tropical to temperate, rainforest to desert. One would have to conclude that *Selaginella* is indeed an evolutionary success story. The longevity and apparent success of *Selaginella* is even more remarkable given its rather simple morphology. In the present paper an attempt has been made to call attention to certain structural features that may hold the key to a better understanding of the evolutionary status of *Selaginella*. If the basic morphology of *Selaginella* has remained essentially unchanged since the Carbonif-

erous, then the study of extant forms of *Selaginella* should yield insights into certain aspects of early land plant evolution. Developmental studies on such enigmatic structures as the ligule, "rhizophore," and angle-meristem, and phenomena such as anisophylly, monoplastidy, and heterospory may be as relevant to the evolutionist as to the developmental botanist. Modern selaginellas lend themselves to experimentation. They are readily grown and manipulated under greenhouse and laboratory conditions. Through continued developmental studies of the vegetative and reproductive organs of *Selaginella*, insights may be gained into some of the reasons underlying the longevity and survival of this unique group of plants. Coupled with the study of extant forms should be a reinvestigation of existing fossil material of *Selaginella* to determine the extent to which the genus has changed in its morphological and anatomical details through the ages. Whether the genus *Selaginella* represents an evolutionary dead end or a group that led to higher plant forms, its modern and past history is interesting and offers ample opportunity for fruitful research in the future.

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THE MESOZOIC HERBACEOUS LYCOPSIDS

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Abstract

Occurrences of lycopsid megafossils and their spores in the Mesozoic are reviewed. Subarborescent lepidodendralean forms diversified in the early Mesozoic before going extinct in the early Jurassic, although herbaceous, *Isoetes*-like forms—considered here also to be lepidodendraleans—survived to the present day as represented by the sole surviving genus *Isoetes*. Records of *Isoetes*-like forms from Triassic strata are considered questionable; the earliest good-quality examples that can currently be accepted are in the late Jurassic/early Cretaceous. The two other major groups of lycopsids that also survive today—the lycopodialeans and selaginellaleans—were present throughout the Mesozoic as entirely herbaceous forms. Some of them closely resemble extant species but most are less similar and some, such as *Synlycostrobus* with its apparently compound strobili, greatly extend our knowledge of lycopsid diversity. A few of the Mesozoic species appear to provide important and hitherto unsuspected links between these two major groups. Increasingly refined knowledge of late Paleozoic through Mesozoic lycopsids and their spores is contributing to growing precision in biostratigraphy and also in environmental changes that have affected our planet in the geological past, particularly the protracted interval of global warming that began in the late Paleozoic and continued throughout the Mesozoic. New information is presented on Mesozoic lycopsids from the United States and England, including a new species of *Isoetites* of Cretaceous age with well-preserved spores in situ.

The late Paleozoic through Mesozoic was an exciting time of transition between ancient and modern floras, bridging the gap between the Paleozoic, which had relatively few plants like those we know today, and the Tertiary (especially the late Tertiary), by which time many plants were essentially modern in appearance. Lycopsids did not escape this phase of intense biotic change; within the Mesozoic timespan of 170 million years the great tree lycopsids of the Paleozoic, i.e., the lepidodendraceans and other families, finally died out, leaving only the diminutive *Isoetes*-like forms to survive to this day. These sole survivors, still largely inhabitants of pools and swamps, bear witness to a once mighty group of swamp-forest and lacustrine organisms. On the other hand the Selaginellales and Lycopodiales, which also had their origins in the Paleozoic, continued to diversify throughout the Mesozoic as indeed they still do today. They were represented by a core of forms similar to extant species with a range of extinct forms that were more or less intermediate and some that are simply bizarre. These evolutionary changes that took place in the Mesozoic were results of global environmental changes, especially the intense climatic warming that occurred between the glaciations of the late Paleozoic and the greenhouse conditions that mark most of Mesozoic time. The dramatic effects of this warming on arborescent lycopsids in the Pennsylvanian, the Permian, and especially the early Mesozoic provide an excellent example of how ancient plants can be used as mirrors of ancient climate change, and, in the case of lycopsids, also of edaphic change. Conversely, an understanding of the effects of climatic change on ancient vegetation is contributing to increasing precision and sophistication in our awareness of how plant ecosystems have changed and developed through geologic time.

The detailed picture of lycopsid evolution in the Mesozoic is currently far from complete. The paleobotanical data base needs focussed attention if we are to appreciate relationships and climate-related global changes in vegetation through geologic time. In Mesozoic lycopsids much important material languishes unexploited in museum cabinets, while poor or poorly described material has been widely and rather uncritically accepted as providing satisfactory evidence, for example of the appearance of extant taxa such as *Isoetes*. An example to which we will draw attention in this survey is Bock's (1962) record of supposed *Isoetes* from the Triassic of North America. This is not to say that *Isoetes*-like forms definitely did not occur in the Triassic; what we conclude is that the evidence as currently expressed in the literature is unconvincing. There are many other such instances where a critical reexamination of the orig-

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inal material is needed, using modern laboratory techniques and fresh collecting.

Although this means that Mesozoic lycopsids present an especially promising area for research, they also represent an area beset with a number of challenging problems. First, although lycopsids are not especially uncommon in Mesozoic rocks (though much scarcer than in the Carboniferous), relatively few occurrences are of the quality of preservation needed to identify the material as lycopsid, let alone to characterize it properly; many of the plants were herbaceous forms that tend not to fossilize well, and important characters for their classification, such as the presence or absence of a ligule on the leaf, can be notoriously difficult to assess. As noted by Seward (1910), there is danger of confusion between lycopsids and such other contemporary groups of plants as conifers and bryophytes, when not enough characters can be seen. Second, this problem is exacerbated in the lycopsids by an asymmetry in the quality and quantity of preservation of dispersed spores versus megafossils, and conversely by the importance of in situ spore characters in identifying and characterizing megafossils. There is a wide diversity and rich abundance of dispersed megaspores worldwide throughout the Mesozoic, but the affinities of many of them remain obscure in the absence of knowledge of the megafossils and hence of the plants that produced them. Equally, there are many records of heterophyllous *Selaginella*- and *Lycopodium*-like megafossils of which the exact affinities can only be determined by reference to evidence from in situ spores as well as their vegetative characters. However, although there is an argumentatively tight circle here, it is not in practice a vicious one. The real problem is that good-quality megafossils in which both spores and vegetative parts are well preserved are uncommon, and, of those that are known, few have as yet been documented adequately using modern techniques. The solution lies in focussing future work on quality megafossils that have in situ spores preserved.

A primary objective of any review is to present and summarize the information that is reasonably well known, representing achievements that have already been made. There have been considerable advances both in the breadth and depth of knowledge of Mesozoic lycopsid diversity in recent years. Moreover, although important recent studies of Paleozoic lycopsids have cast doubt on Mägdefrau's (1956) simple picture of the arborescent lepidodendraleans evolving by reduction through *Pleuromeia* and *Nathorstiana* to *Isoetes* (see also Chaloner & Boureau, 1967), there is no doubt that whatever their botanical affinities, the intense global warming of the late Paleozoic and early Mesozoic led to the extinction of all arborescent and subarborescent lycopsids, at first in the then equatorial everwet regions sensu Ziegler (1990). All currently known fossil species of lycopsids surviving into or newly evolving in the mid-Jurassic through Cretaceous were herbaceous, at least to the extent that all extant lycopsids can be regarded as herbaceous. Among the objectives of the review, therefore, is an attempt to comment critically on available records as reported in the literature, so far as is possible without direct examination of the specimens themselves, and thus to focus on especially worthwhile material for future research (whether from renewed collecting or in existing collections). Utilizing our own research material, an additional objective is to illustrate directly the range in quality of preservation of Mesozoic material and some of the successes as well as difficulties attendant on its study. Reflecting the major floristic change, this review begins with the mainly subarborescent lepidodendralean forms of the early Mesozoic, followed by a discussion of the dispersed spore record of Mesozoic lycopsids in general and then by the herbaceous fossils of the Lycopodiales and Selaginellales, which are mostly of later Mesozoic age, and ending with Isoetales and allied forms. Thus, the *Isoetes*-like lepidodendraleans are treated separately from the arborescent ones, on purely arbitrary grounds. The review is concluded with a brief discussion on phylogenetic relationships.

The Subarborescent Lepidodendraleans of the Early Mesozoic (Triassic–Early Jurassic)

Annalepis-Lepacyclotes

Annalepis is represented by large, well-preserved sporophylls with pointed apices, 2.5–4.5 cm long, 1–2 cm wide, described in detail from the middle Triassic of France by Grauvogel-Stamm & Duringer (1983). The sporophylls are monosporangiate and have yielded either megaspores of *Tenellisporites/Dijkstraisporites* type or monolete microspores referable to *Aratrisporites*, a miospore (spore less than 200 μm, see Traverse, 1988) that is stratigraphically useful and which occurs widely as a dispersed spore in Triassic rocks. Although the authors' estimate of at least 14 cm diameter for the reconstructed strobilus may be too large, the cone was certainly no less than 9 cm wide at its widest point and thus represents the largest of any known Mesozoic lycopsid. Comparable but less complete and somewhat smaller sporophylls from China, also with in situ spores, have